

ANISOCNEMUS, A NEOTROPICAL GENUS:
CLASSIFICATION AND GEOGRAPHICAL DISTRIBUTION
(COLEOPTERA: CARABIDAE: HARPALINI)

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ABSTRACT

Adults of this genus are distinguished from those of other selenophorines by a combination of front tibia markedly broadened with crenulate outer margin, and elytral striae 2 and 5 each with a row of setigerous punctures. Adults of the two allopatric species of *Anisocnemus* are distinguished from one another by differences in form of the pronotum and by presence or absence of adhesive vestiture on the ventral surfaces of the middle tarsi of males. *A. validus* Chaudoir, 1843, is known only from northeastern South America (Venezuela), and *A. amblygonus*, new species (type locality—Mexico, Oaxaca, La Ventosa), ranges from the Tropic of Cancer on the Pacific coast of Mexico to northwestern South America. Relationships of *Anisocnemus* cannot be detailed because the probable sister group was not identified. The suggested pattern of evolution is: origin of a stock with adults adapted for burrowing in the lowland tropics of northern South America; dispersal in late Tertiary or early Quaternary, followed by isolation in separate refugia of the descendants of the original dispersing stock; differentiation, followed by re-dispersal. The northernmost stock which gave rise to *A. amblygonus* may have survived either in a refugium in northernmost South America, or else in one in Middle America. Because adults fly readily, dispersal into Middle America could have occurred before that area and South America were connected by a land bridge.

At La Ventosa, Oaxaca—the place of the winds—beside the main highway that crosses the Isthmus of Tehuantepec, is a rather dingy establishment, including a gas station and a restaurant with clanging metal doors and louvered windows. It is an oasis: a watering hole where field biologists and their vehicles can obtain necessary sustenance, and can rest during the day, shaded from the sun and protected from the winds that blow seemingly unremittingly, across this cut-over, semi-desolate tropical lowland plain. It is a place to rest, and for the outbound travellers from the north, a place to contemplate and anticipate fine collecting to the east, in the Neotropical Chiapan highlands, but with expectations tempered by recent experiences in the Oaxacan sierras, some 100 kilometers to the west.

How insects manage to fly in the windy conditions that prevail in this country seems something of a mystery: but, fly they do, and, attracted at night by the lights of the gas station, they gather near the walls of the restaurant, and on the gravel, near the gas pumps. Conspicuous among such hexapod refugees from the winds are rather bulky selenophorines of the genus *Anisocnemus*. They are ignored or carelessly squashed underfoot by those who man the gas pumps, but they are seized and preserved by certain biped refugees from the winds: the coleopterists. It was here that the junior author first encountered these beetles as living organisms. They and their relatives are the subject matter of this paper.

Relationships of the nine selenophorine genera that inhabit the tropical and temperate parts of the New World are not well understood—nor will they be, until the most diverse genera of the group, *Selenophorus* Dejean and *Athrostictus* Bates, have been studied in detail. Completion of such a task is not near at hand, though work is in progress on the Middle American species of *Selenophorus*. In the meantime, it seems desirable to review some of the less diverse groups, to provide experience and background information for the more extensive studies. To this end, the junior author published two papers about the species and characteristics of *Aztecarpalus* (Ball 1970, 1976). Here we treat similarly *Anisocnemus* and its species.

The senior author undertook the work necessary to characterize the taxa, studied geographical variation, and prepared the tables, illustrations, and a first draft of the text. To the latter, the junior author added notes about types, based on his observations, and wrote the introduction and sections about relationships and evolution.

ACKNOWLEDGMENTS

We are pleased to record our appreciation for the loan of specimens received from the curators whose names and institutions are listed below, in the "Materials" section. The junior author expresses his appreciation to A. Bons and J. Menier, Entomologié, Museum National d'Histoire Naturelle, Paris, for generous assistance and hospitality rendered during his stay there, in the late winter and early spring of 1972. He also remembers with pleasure the rest stops at La Ventosa, shared at one time or another over a period of ten years with Donald R. Whitehead, Terry L. Erwin, Robin E. Leech, Kathleen E. Ball, Peter A. Meyer, Bruce S. Heming, and Henry E. Frania. Each of these individuals contributed to the material basis of this paper by collecting specimens of *Anisocnemus*.

The SEM photographs were taken by George Braybrook, and the final version of the typescript was typed by Twyla Gibson. J. S. Scott prepared the plates. B. S. Heming and J. S. Ashe carefully reviewed the text. We also thank Gloria N. House, USNM, for adding Central American locality records of *A. amblygonus* to the distribution map and Anne L. Halpern for re-typing corresponding text pages to accommodate the newly added localities.

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MATERIALS AND METHODS

Material. This comprises 564 adults of *Anisocnemus*, plus a few selected specimens of each of the other New World selenophorine genera. Some of the *Anisocnemus* specimens were collected by the junior author and various field companions, but most were borrowed from the institutions listed below. Acronyms associated with names of institutions are used in the text to indicate sources of specimens.

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| AMNH | American Museum of Natural History, New York, N.Y. 10024, L. H. Herman, Jr. |
| CAS | California Academy of Sciences, San Francisco, Calif. 94118, D. H. Kavanaugh |
| FDAG | Florida Dept. of Agriculture, Gainesville, Fla. 32601, R. E. Woodruff |
| FMNH | Field Museum of Natural History, Chicago, Illinois 60605, H. Dybas |

MCZ	Museum of Comparative Zoology, Cambridge, Mass. 02138, J. C. Scott
MNHP	Museum National d'Histoire Naturelle, Paris, A. Bons
OSUC	Oregon State University, Corvallis, Oregon 97331, P. O. Ritcher
TAMU	Texas A&M University, College Station, Texas 77840, H. R. Burke
UAIC	University of Arkansas, Fayetteville, Arkansas 72701, R. T. Allen
UASM	University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3
UCD	University of California, Davis, California 95616, R. O. Schuster
USNM	Smithsonian Institution, Washington, D.C. 20560, R. D. Gordon, T. L. Erwin

Methods. These are standard. Measurements described below were made with an ocular micrometer mounted in a Wild M5 stereobinocular microscope, at a magnification of 12 diameters.

Length of head—linear distance from base of clypeus to posterior margin of compound eye.

Width of head (Hw)—linear transverse distance across head and eyes.

Length of pronotum (Pl)—linear distance along mid-line from base to apex.

Maximum width of pronotum (Pmw)—greatest transverse distance across pronotum.

Pronotum, width at base (Pbw)—linear distance between hind angles.

Pronotum, width at apex (Paw)—linear distance between anterior angles.

Length of elytra (El)—length of longer elytron, from basal groove to apex.

Size was expressed as Standardized Body Length (SBL), and is the sum of Length of Head, Pl and El. The following ratios were calculated: Hw/Pl; Hw/Pmw; Pbw/Pmw; Paw/Pmw; Pl/Pbw; and Pl/El. In order to determine the nature and amount of geographical variation in *A. amblygonus* new species, standard statistics were calculated for SBL and these ratios, and are presented in Tables 1 and 2 for population samples collected at Tehuantepec, Mexico, and at Valledupar, Colombia. These localities were chosen because they are widely separated, and each was represented by enough specimens to make statistical analysis worthwhile.

The following ratios were calculated for comparison with those of other genera, and are included only in the description of *Anisocnemus*:

length of longer spur of hind tarsus/length of hind basitarsus (article 1), measured on the dorsal surface.

Scape-Tarsal ratio—for males, length of antennal scape/width of front tarsomere 4. This is an indication of the relative width of the front tarsal articles of males.

Illustrations were made with the aid of a camera lucida mounted on a Wild M5 stereobinocular microscope. The scale markings represent one mm. for all illustrations. Because diagnostic features of the genus and its two species are so simple, illustrations clearly indicate the diagnostic features of these taxa. Thus, keys seem unnecessary and are not provided. Also, the descriptions of the species are very brief, and they should be studied in conjunction with the more extensive characterization of the genus.

RECOGNITION AND RANKING OF TAXA

This group is ranked as a genus because of the amount of structural divergence in form of the front tibiae between the included species and those included in other selenophorine genera. Additional criteria involve monophyly (the two species of *Anisocnemus* are so similar to one another that they must be descended from an immediate common ancestor, and the taxa exhibit a contiguous geographical range), and occupation of a distinctive

adaptive zone (*Anisocnemus* adults are probably burrowers in soil). Further work may show a sister-group relationship between *Anisocnemus* and one of the species groups included in *Selenophorus*. If so, the two genera should be combined, but for the present, we prefer to recognize these taxa as generically different.

The basis for recognizing species is that two allopatric forms are clearly distinguished from one another by marked differences in two characters. Though allopatric, the ranges of the two groups are sufficiently close to suggest that either intermediates do not exist, or if they do, they are confined to a narrow zone. Thus it seems reasonable to infer that the two forms are either reproductively isolated or almost so, and therefore qualify as distinct species.

CLASSIFICATION AND DESCRIPTION

Anisocnemus Chaudoir, 1843

Anisocnemus Chaudoir, 1843:394. Lacordaire, 1854:295. Csiki, 1932:1194. Van Emden, 1953:516.

TYPE SPECIES: *Anisocnemus validus* Chaudoir, 1843:394. (By monotypy).

A combination of three structural features distinguish adults of *Anisocnemus* from those of other selenophorine genera: more or less cylindrical body form; elytral striae 2 and 5 each with a row of setigerous punctures; and front tibia expanded, with outer margin crenulate. Additionally, the latter structures are sexually dimorphic (Figs. 1a and 2). Males have two groups of spines in the internal sac (Figs. 15 and 16), and females have a markedly enlarged abdominal sternum 10 (Fig. 21).

The convex body form of adult *Anisocnemus* is shared by specimens of *Discoderus* LeConte, which also have slightly expanded front tibiae; males of *Discoderus* are without adhesive vestiture on the ventral surfaces of the middle tarsi, and females have a larger sternum 10 than seems normal for selenophorines. However adults of *Discoderus* differ from those of *Anisocnemus* in the following features: the elytra have setigerous punctures in stria 7 as well as in striae 2 and 5, the front tibiae are not sexually dimorphic, and males have bowed middle tibiae. Furthermore, because the vestiture of the middle tarsi of males varies inter-specifically in *Anisocnemus*, it seems likely that bare middle tarsi were evolved independently in males of this genus and in those of *Discoderus*.

Adults of *Stenomorphus* Dejean have setigerous punctures in only striae 2 and 5, and males are without vestiture on the ventral surfaces of the middle tarsi; but the front tibiae are not markedly expanded, the prothorax is markedly elongate, males lack armature of the internal sac, and females have a bifurcate stylus of the ovipositor.

Adults of most species of *Trichopselaphus* Chaudoir have setigerous punctures in only striae 2 and 5, and males lack vestiture from the middle tarsi, but the front tibiae are normal, armature of the male internal sac is unique, and sternum 10 of females is average.

Adults of *Amblygnathus* Dejean, *Selenophorus* Dejean, and *Gynandropus* Dejean have punctures in striae 2, 5 and 7, the front tibiae are not expanded, and the body form of most adults is normal, rather than subcylindrical. These same features characterize adults of *Athrostictus* Bates, in which, additionally, the dorsal surface of the elytra is more or less punctate and hairy.

Adults of *Aztecarpalus* Ball lack setigerous punctures from striae 2, 5, and 7, armature of the male internal sac differs from that of male *Anisocnemus*, and sternum 10 of females is not greatly enlarged.

Description. Standardized Body Length 9.83-15.42 mm. Body subconvex dorsal surface glabrous, but with setigerous punctation in stria 2 and 5, and with usual fixed setae.

Color. Body piceous to black, elytra faintly bronze to black. Antennae, mouthparts, and legs piceous to rufo-piceous.

Microsculpture. Mesh pattern isodiametric except slightly transverse on elytra; meshes faint on head and disc of pronotum.

Luster. Moderate, shining, faintly bronze.

Head. Labrum as in Fig. 3. Frontal impressions punctiform. Eyes small, subgena at least two times wider than antennal scape. Antennae short, length less than distance from base of antennae to base of pronotum. Mandibles (Fig. 4) thick; in closed position right mandible overlapped by left. Molar area and ventral groove with short hairs. Left mandible (Fig. 4a) with cutting edge formed by retinacular ridge; terebral tooth broad; posterior retinacular tooth in form of prominent ridge; premolar tooth small. Right mandible (Fig. 4b) with cutting edge formed by terebral ridge, terebral tooth small; anterior retinacular tooth large; premolar tooth small. Maxillae as in Fig. 5. Labium as in Fig. 6; mentum with prominent lateral lobes. Ligula with glossal sclerite elongate, widened toward apex, with two setae near apex; paraglossae broad, glabrous, membranous (Fig. 6).

Prothorax. (Figs. 7 and 8). Pronotum transverse, markedly convex; anterior margin shallowly to moderately concave, posterior margin about straight; sides rounded, not sinuate posteriorly, or distinctly sinuate; anterior angles broadly rounded; posterior angles broadly obtuse, or rectangular. Anterior and posterior impressions present; median longitudinal impression shallow; posterior lateral impressions moderate to deep basins.

Pterothorax. Metepisternum elongate, lateral margin longer than anterior margin.

Elytra. Convex, sides slightly rounded, humeri angulate; subapical margins feebly or moderately sinuate. Striae moderately impressed. Striae 2 and 5 each with four setigerous punctures.

Legs. Anterior tibia expanded (more so in males than in females), outer margin crenulate, (Figs. 1a and 2). Apical spur of front tibia more or less widened (Figs. 1a and 2). Hind basitarsus short (length of tarsal spur/length of hind basitarsus: 1.00), shorter than combined length of tarsal articles 2 and 3. Anterior tarsus of males moderately broad (Scape-Tarsal Ratio: 2.00). Males with adhesive vestiture ventrally on front and middle tarsomeres (Figs. 9 and 10), or only on front tarsomeres (Figs. 11 and 12). Female tarsi without adhesive vestiture (Fig. 13).

Hind wings. Fully developed, with clear membrane and small wedge cell (Fig. 14).

Abdomen. Sternum 2 and 5 with fine sparse hairs medially; sternum 2-5 each with one pair of large setae medially; sternum 6 of male and female with four ambulatory setae (anal setae).

Male genitalia. (Figs. 15 and 16). Median lobe tubular, with dorsal membranous area extended almost to basal bulb; narrowed apically; eversion point of internal sac mediad. Internal sac with two groups of ten spines visible laterally and ventrally. Parameres as in Fig. 17.

Ovipositor and associated sclerites. Tergum and sternum 8 as in Figs. 18 and 19. Tergum 10 (proctiger) with apical margin slightly sinuate (Fig. 20). Sternum 10 moderately sclerotized (Fig. 21). Valvifer falciform apically, apex rounded, spine moderate (Fig. 22). Coxite elongate with moderate spines near inner apical margin (Figs. 22). Stylus falcate (Fig. 22).

Female genitalia. No vaginal sclerite.

Derivation of generic name. Greek, *aniso*-unequal; *kneme*-leg between knee and ankle. Evidently the name alludes to the striking difference in form between the front and middle and hind tibiae.

Geographical distribution. The range of this genus extends from the Tropic of Cancer on the Pacific coast (Mazatlan, Mexico) southward through Central America to the Atlantic coast of northern South America (Colombia and Venezuela), as in Fig. 23.

Anisocnemus validus Chaudoir

Anisocnemus validus Chaudoir, 1843:394. LECTOTYPE (here selected), male, labelled: Ex Musaeo Chaudoir; LECTO TYPE; det. G. E. Ball '72. In Oberthür Collection, Box 205, second specimen in row in front of this box label: *validus* Chaudoir Colombie Mus. de Berlin [MNHP]. Type area—Colombia. Lacordaire, 1854:295.

Note about type material. In the original description, Chaudoir recorded that the material of *A. validus* was collected in Colombia, and was received from Mannerheim and the Berlin Museum. (It is important to realize that at that time, Venezuela did not exist as an independent country, but was part of Colombia). Two features mentioned by Chaudoir establish conspecificity between the material presently associated with the box label in the Oberthür collection and the original description: pronotum with sides sinuate, hind angles rectangular (description of *A. validus*); and article 4 of middle tarsus of male with spongiöse pubescence ventrally (description of *Anisocnemus*).

Description. Standardized Body Length: male 13.17 mm; female 12.08 mm. Characteristics as in description of genus. Pronotum as in Fig. 7, with hind angles rectangular, and front and middle tarsomeres of male with adhesive vestiture ventrally (Figs. 9 and 10). Male genitalia and terminal abdominal sclerites and ovipositor of female as in Figs. 15-22.

Material examined. We have seen two specimens of this species. The male is labelled Venezuela, Valleo de Aragua, and the female is labelled Venezuela. Both specimens are from the MNHP, and were compared with type material of *A. validus* Chaudoir. Both specimens were dissected.

Anisocnemus amblygonus Shpeley and Ball, new species

Comparison. Specimens of this species differ from those of *A. validus* in pronotal form: hind angles are rounded, and the sides are not sinuate posteriorly (Fig. 8); and males are without adhesive vestiture on the ventral surfaces of the middle tarsal articles (Figs. 11 and 12).

Description. Standardized Body Length: males 9.83-15.42 mm females 10.92-14.75 mm. Body proportions exemplified by two samples, with data presented in Tables 1 and 2 for variation in: Hw/Pl, Hw/Pmw, Pbw/Pmw, Paw/Pmw, Pl/Pbw, and Pl/El. Characteristics as in description of genus. Pronotum as in Fig. 8, ventral surfaces of tarsomeres of middle tarsus without adhesive vestiture (Fig. 12). Elytron with subapical margin more sinuate than in *A. validus*. Male genitalia as in Figs. 15-17, terminal abdominal sclerites and sclerites of ovipositor as in Figs. 18-23. Six males and seven females were dissected.

Variation. Because all specimens of *A. amblygonus* are markedly similar to one another, an extensive analysis of variation was not undertaken. Comparisons of a population sample from Tehuantepec, Mexico with one from Valledupar, Colombia show statistically (but not taxonomically) significant differences for both males and females in SBL, and all ratios in Tables 1 and 2 except Paw/Pmw and Pl/El. These data illustrate that widely separated populations are only slightly different from one another. Structural features of geographically intermediate populations probably bridge the differences between the Tehuantepec and Valledupar samples.

Derivation of name. From Greek *amblys* meaning obtuse, and *gonia* meaning angle; in allusion to the obtuse posterior angles of the pronotum.

Material examined. We have seen 546 specimens of this species; 16 additional specimens were determined by T. L. Erwin and their data added

TABLE 1: DATA ON VARIATION IN STANDARDIZED BODY LENGTH AND SELECTED PROPORTIONS FOR MALES OF TWO POPULATION SAMPLES OF *Anisocnemus amblygonus*, NEW SPECIES

		MALES					
	Group	N	Range	\bar{x}	1.5 SD	2 SE	C.V.
SBL	Oaxaca ¹	15	12.50-15.42	14.01	1.16	0.40	5.49
	Magdalena ²	15	11.17-13.58	12.21	1.25	0.44	6.83
Hw/P1	Oaxaca	15	0.80- 0.91	0.85	0.05	0.02	3.56
	Magdalena	15	0.84- 0.95	0.90	0.06	0.02	3.97
Hw/Pmw	Oaxaca	15	0.61- 0.68	0.64	0.03	0.01	2.95
	Magdalena	15	0.66- 0.71	0.68	0.03	0.01	2.33
Pbw/Pmw	Oaxaca	15	0.83- 0.89	0.86	0.03	0.01	2.10
	Magdalena	15	0.79- 0.86	0.83	0.03	0.01	2.44
Paw/Pmw	Oaxaca	15	0.66- 0.72	0.68	0.03	0.01	2.40
	Magdalena	15	0.66- 0.73	0.69	0.03	0.01	2.66
P1/Pbw	Oaxaca	15	0.83- 0.89	0.87	0.03	0.01	2.36
	Magdalena	15	0.85- 0.94	0.91	0.04	0.01	2.79
P1/E1	Oaxaca	15	0.43- 0.47	0.45	0.02	0.01	2.44
	Magdalena	15	0.44- 0.47	0.46	0.02	0.01	2.45

¹ Tehuantepec, Mexico.² Valledupar, Colombia.

during editorial preparation. The holotype (male) and allotype are labelled as follows: La Ventosa, Oaxaca, MEXICO, 6.VIII.63- at light Whitehead & Woodruff. The paratypes are labelled as follows: same as holotype [UASM] (55); MEXICO, Oaxaca, La Ventosa, U-V light, 6.VIII.1963, R. E. Woodruff [UASM] (30); La Ventosa, Oaxaca, MEX., 20.VII.63, at lights, Ackerman & Whitehead [UASM] (2); Mex., Oaxaca, La Ventosa, VIII.28.1967, Ball, Erwin, Leech collectors [UASM] (1); La Ventosa Junct., Oaxaca, Mexico, V.26.1969, H. F. Howden [UASM] (1); Tehuantepec, Oax., Mexico, Aug. 10, 1963, Scullen & Bolinger col. [OSUC] (67); and MEX., Oaxaca, Tehuantepec, VI.II-1964, J. C. & D. Pallister col. [AMNH] (162).

The holotype and allotype are in the entomological collections of the USNM. In addition to the institutes indicated above, paratypes are in the following collections: British Museum of Natural History; Canadian National Collection; Instituto Politecnico de Mexico, and the University of Arkansas, Fayetteville.

The remainder of the material examined was from the following localities:

MEXICO. *State of Sinaloa*: 3 km e Mazatlan, 16.VIII.54, R. Ryckman, C. Christianson, R. Lee, [USNM] (1); Mazatlan, 22.VII.54, M. Cazier, W. Gertsch, Bradts [AMNH] (5); Mazatlan, 2.VIII.53, C.&P. Vaurie [AMNH] (1); Mazatlan, collected at light, 17-23.VII.63, P. J. Spangler [USNM] (1). *State of Jalisco*: 10.6 mi s La Huerta, Rte. 80, 1000'. 4.VIII.66, George E. Ball, D. R. Whitehead [UASM] (5); 23.2 mi s Autlan, 800', Rte. 80, 5.VIII.66, George E. Ball, D. R. Whitehead [UASM] (2). *State of Colima*: Vulcano, L. Conrad [USNM] (21); 16.5 mi e Colima, 1900', Rte. 110, 2-3.VIII.66, George E. Ball, D. R. Whitehead [UASM] (2); Colima, at light, 1500', Rte. 110, 2-3.VIII.66, George E. Ball, D. R. Whitehead [UASM] (1); 12.8 mi e Manzanillo, sea level, u-v light, 5.VIII.67, Ball, T. Erwin, R. E. Leech [UASM] (1); 8 mi sw Colima, impoundment, 25.VII.63, Ackerman & Whitehead [UASM] (1); Colima, Conradt [USNM] (1). *State of Guerrero*: El Marques, 28 km e Acapulco, 18.VII.57, Wm. W. Gibson [UASM] (13); Acapulco, 18.VIII.38, Lipovsky [MCZ] (4); Acapulco, I.VII.51, H. E. Evans [UASM] (2); Acapulco, 20.VII.51, M. Quigley [UASM] (1); Acapulco, 8.VIII.36, C. H. Seevers [FMNH] (1); Iguala, Wickman [MCZ] (1). *State of Oaxaca*: Tehuantepec, 12.VII.55, P.&C. Vaurie [AMNH] (22); Hotel Tehuantepec, 18.VIII.63, H. V. Weems, Jr. [FDAG] (9); Tehuantepec Hotel, u-v light, 6.VII.63, R. E. Woodruff [UASM] (8); Tehuantepec, 1.IX.59, [TAMU] (2); Tehuantepec, 5.VIII.65, Flint & Oritz [USNM] (1); 6 mi w Tehuantepec, taken at light, 6.VII.71, Clark, Murray, Hart, Schaffner [TAMU] (2); Tehuantepec, at light, 5.VI.65, Burke, Meyer, Schaffner [TAMU] (1); 6 mi w of Jalapa de Marques, taken at light, 23.VII.73, Mastro & Schaffner [TAMU] (2); Rte. 200, 3.6 mi w Rio Grande, palm forest, u-v light, 17.VII & 7-8.VIII.72, B. S. Heming, G. E. Ball [UASM] (2); Ixtepec, II.IX.47, B. Malkin [AMNH] (1); Salina Cruz, 12.VII, Fred K. Knab [USNM] (2); Salina Cruz, 18.VII, Fred K. Knab [USNM] (4). *State of Chiapas*: 65 km s of Tuxtla Gutierrez along rd. to Nueva Concordia, 823 m, 12.IX.74, D. E. & J. A. Breedlove [CAS] (5); 44.1 mi e Comitán, Rte. 190, 2100', 3.IX.65, George E. Ball, D. R. Whitehead [UASM] (4); 32.5 mi e Comitán, Rte. 190, 2200', blacklight, 3.IX.65, George E. Ball, D. R. Whitehead [UASM] (2); Puerto Madero, ca. sea level, u-v light, 1.VIII.72, G. E. Ball [UASM] (2); 4.9 mi n Frontera-Comalapa, 2400', 2.IX.67, Ball, T. L. Erwin, R. E. Leech [USAM] (1); 96 km s Tuxtla Gutierrez on rd. to Nueva Concordia nr jct. with rd. to Mapastepec, 732 m, 10.X.74, D. E. & J. A. Breedlove [CAS] (1); 10 mi nw Arriaga nr. Rio Las Arenas, 122 m, 27.VIII.74, D. E. & J. A. Breedlove [CAS] (1). GUATEMALA. Managuá, V.52, Wm. T. Miller [CAS] (1). EL SALVADOR. 4 mi n Quezaltepeque, 19.VII.61, M. E. Irwin [UCD] (1). Santa Tecla, 8.IX.56, P.A.B. [USNM] (1). *Dept. of Sonsonate*, Acajutla, 26.V.64, P. S. Blanton, A. B. Broce, R. E. Woodruff [UASM] (3). NICARAGUA. El Guabillo, Diriamba, 30.VI.76, G. Medrano [USNM] (4). Sebaco, 1900 ft. elev., 7.VII.63, Scullen & Bolinger [OSUC] (1). Tipitapa, VII.71, J. Maldonado [USNM] (1). COSTA RICA. Playa del Coco, 24.VII.65, R. T. Allen [UAIC] (1). Zapotal, VI.34, Charles H. Ballou [USNM] (3). *Guanacaste Prov.*, V.34, F. Nevermann [USNM] (1); Santa Elena, VI.24, F. Nevermann [USNM] (1). COLOMBIA. *Dept. of Atlantico*: Barranquilla [USNM] (2); Puerto Colombia, at light, 23.IX.27, [USNM] (2). *Dept. of Magdalena*: Valledupar, at light, 20-23.V.68, B. Malkin [FMNH] (50); Valledupar, 22-24.V.68, B. Malkin [FMNH] (27); Cesar, Valledupar, 4-9.VI.68, B. Malkin [FMNH] (7).

Geographical distribution. The range of this species extends in the lowland tropics from northeastern South America to Mazatlan, Mexico, on the Pacific coast (Fig. 23). We have not seen specimens from the Gulf coast of Mexico, although the species should occur there.

Notes about habitat and way of life. Specimens of *A. amblygonus* were collected in Mexico at altitudes between sea level and about 800 meters. The few individuals collected during the day were on damp to saturated clay soil, in palm forest or near roadside ditches and meadows, either under debris, or in burrows in soil. Probably their natural habitat is savanna, or open areas in palm forests. Most specimens, however, were collected at light, at night.

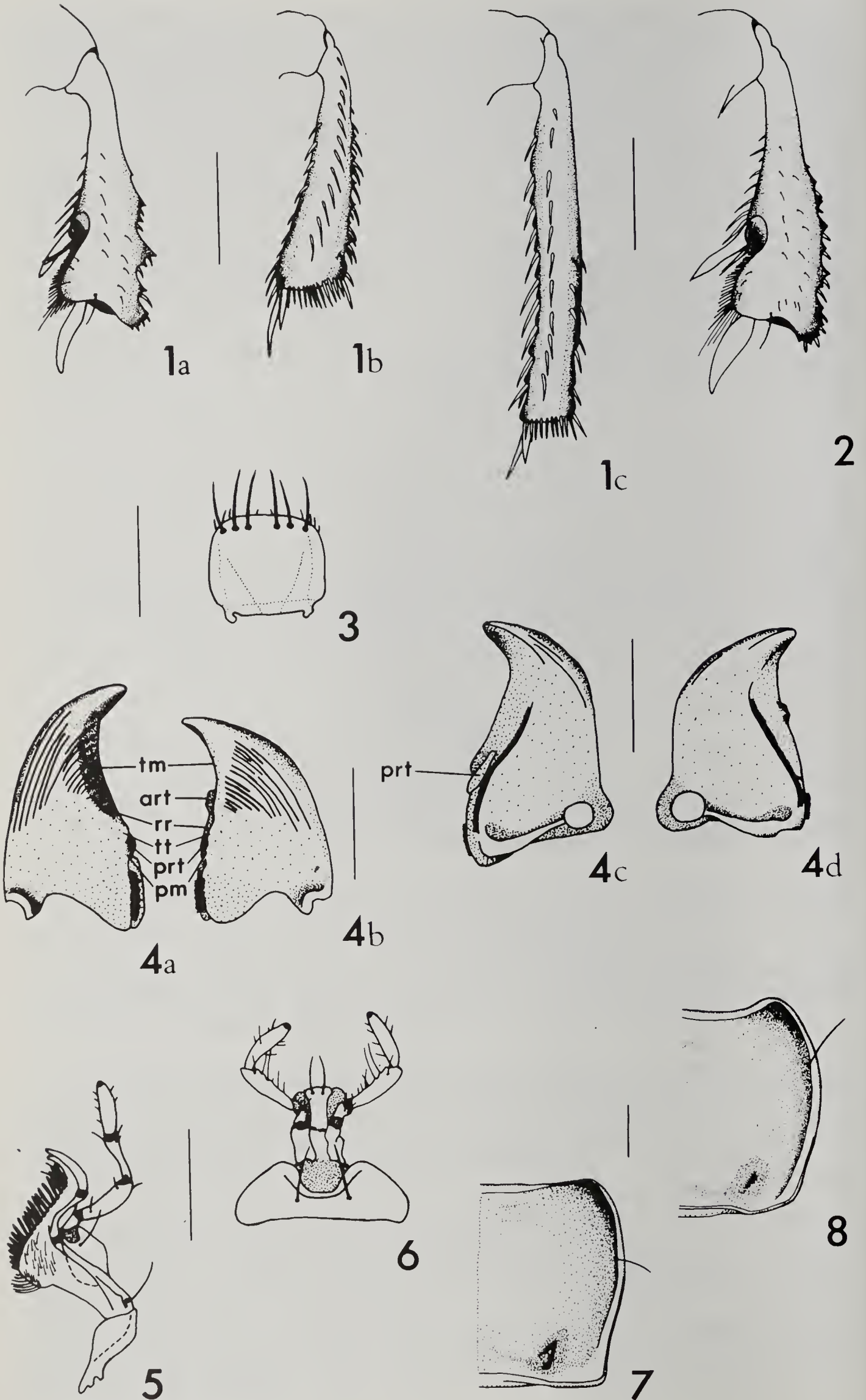
Adults were collected from May 26 to September 23—that is, over the summer months, or the general period of rain in the Mexican tropics. We suggest that the life cycle is timed to produce adults during the rainy season. The few teneral specimens seen were collected in June, July, and August, suggesting that the period of adult emergence is extensive.

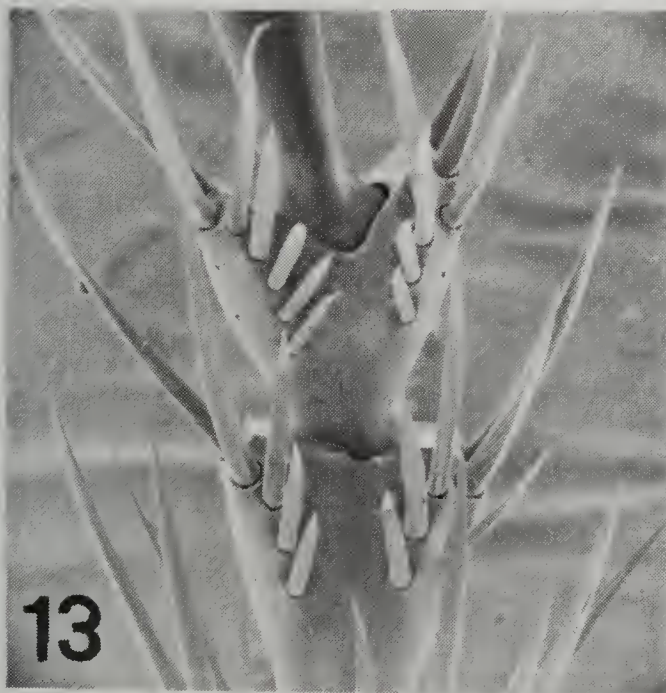
The markedly expanded front tibiae, convex body form, and reduced adhesive vestiture of the male tarsi suggest that these beetles are adapted for burrowing, for these features are shared with other burrowing carabids such as adults of *Discoderus* and *Stenomorphus*. At the locality 44.1 miles east of Comitán, Chiapas, specimens were washed from clay banks by splashing. This suggests that the beetles were in burrows in the soil and tends to confirm burrowing habits.

Judging from the frequency at which adults are found at light, flight is commonly employed as a means of dispersal.

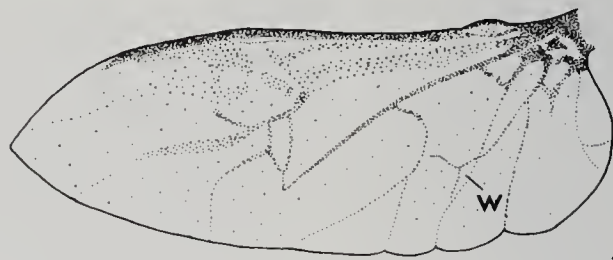
TABLE 2: DATA ON VARIATION IN STANDARDIZED BODY LENGTH AND SELECTED PROPORTIONS FOR FEMALES OF TWO POPULATION SAMPLES OF *Anisocnemus amblygonus*, NEW SPECIES

		FEMALES						
	Group	N	Range	\bar{x}	1.5 SD	2 SE	C.V.	
SBL	Oaxaca	15	11.50-14.75	13.08	1.31	0.44	6.63	
	Magdalena	15	10.92-13.17	12.25	1.11	0.38	6.03	
Hw/P1	Oaxaca	15	0.94- 1.02	0.98	0.03	0.01	2.22	
	Magdalena	15	0.93- 1.05	1.00	0.03	0.01	2.83	
Hw/Pmw	Oaxaca	15	0.67- 0.71	0.69	0.02	0.01	2.01	
	Magdalena	15	0.68- 0.74	0.71	0.03	0.01	2.36	
Pbw/Pmw	Oaxaca	15	0.84- 0.88	0.86	0.02	0.01	1.84	
	Magdalena	15	0.80- 0.87	0.84	0.03	0.01	2.26	
Paw/Pmw	Oaxaca	15	0.69- 0.75	0.72	0.03	0.01	2.41	
	Magdalena	15	0.71- 0.76	0.73	0.03	0.01	2.32	
P1/Pbw	Oaxaca	15	0.78- 0.85	0.82	0.03	0.01	2.43	
	Magdalena	15	0.82- 0.90	0.85	0.04	0.01	3.27	
P1/E1	Oaxaca	15	0.38- 0.42	0.40	0.02	0.01	2.47	
	Magdalena	15	0.40- 0.43	0.42	0.02	0.01	2.86	

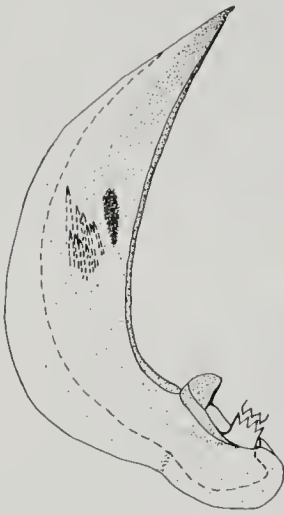




100 μ



14



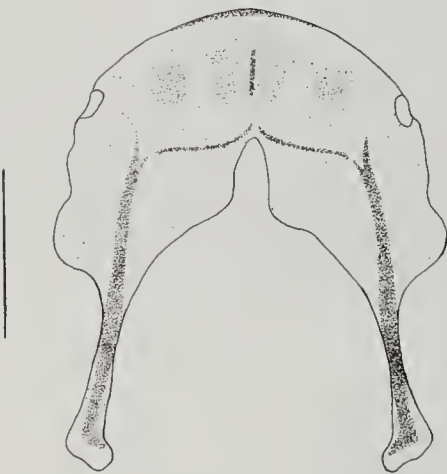
15



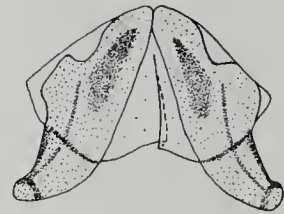
16



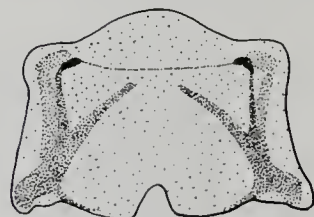
17



18



19



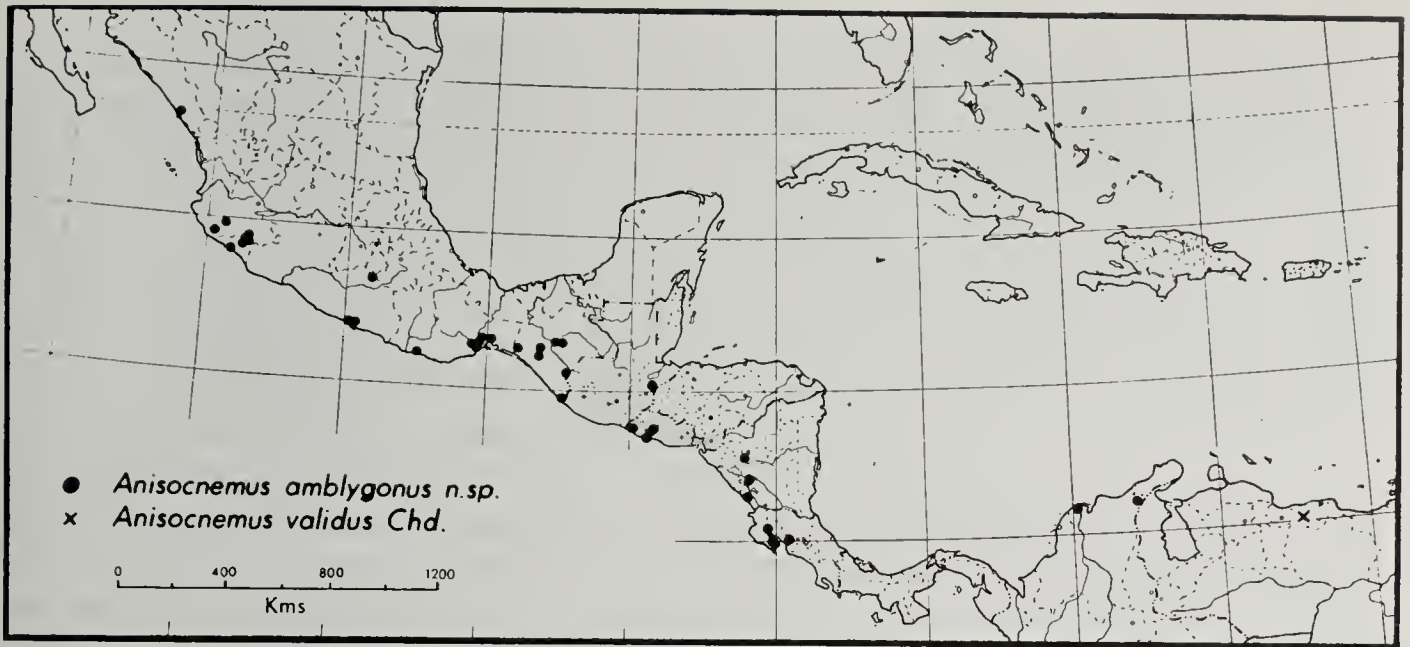
20



21



22



23

CAPTIONS FOR FIGURES

Fig. 1: Left tibiae, anterior aspect, of male of *A. amblygonus*, new species (a, anterior; b, middle; c, posterior; scale marking represents 1 mm, as in all illustrations).

Fig. 2: Left front tibia, anterior aspect, of female of *A. amblygonus*, new species.

Fig. 3: Labrum, dorsal aspect, of *A. amblygonus*, new species.

Fig. 4: Mandibles of *A. amblygonus*, new species (a, left mandible, dorsal aspect; b, right mandible, dorsal aspect; c, left mandible, ventral aspect; d, right mandible, ventral aspect; art--anterior retinacular tooth; pm--premolar tooth; prt--posterior retinacular tooth; rr--retinacular ridge; tm--terebral margin; tt--terebral tooth).

Fig. 5: Right maxilla, dorsal aspect, of *A. amblygonus*, new species.

Fig. 6: Labium, ventral aspect, of *A. amblygonus*, new species.

Fig. 7: Pronotum, right half, dorsal aspect, of *A. validus* Chaudoir.

Fig. 8: Same, of *A. amblygonus*, new species.

Figs. 9-13: SEM photographs of ventral surfaces of tarsomeres. Fig. 9, front tarsus, tarsomeres 1-3, of *A. validus* Chaudoir, male. Fig. 10, middle tarsus, tarsomeres 1-4, of *A. validus* Chaudoir, male. Fig. 11, front tarsus, tarsomeres 1-3, of *A. amblygonus*, new species, male. Fig. 12, middle tarsus, tarsomeres 1-4, of *A. amblygonus*, new species, male. Fig. 13, front tarsus, tarsomeres 3-5, of *A. amblygonus*, new species, female.

Fig. 14: Left hind wing of *A. amblygonus*, new species (W--wedg cell).

Figs. 15-17: Male genitalia of *A. amblygonus*, new species. Fig. 15, median lobe, left lateral aspect. Fig. 16, median lobe, ventral aspect. Fig. 17, parameres, ventral aspect.

Figs. 18-21: Terminal abdominal sclerites of *A. amblygonus*, new species, female. Fig. 18, tergum 8, dorsal aspect. Fig. 19, sternum 8, ventral aspect. Fig. 20, tergum 10, dorsal aspect. Fig. 21, sternum 10, ventral aspect.

Fig. 22: Left valvifer, coxite and stylus of ovipositor, of *A. amblygonus*, new species, female.

Fig. 23: Map of the New World, showing collecting localities for specimens of *Anisocnemus*.

EVOLUTIONARY CONSIDERATIONS

Because information about *Anisocnemus validus*, one of the two species of this genus, is so limited, and because the basis for understanding evolution of selenophorines has yet to be established, it is not possible at this time to make detailed inferences about evolution of *Anisocnemus*. Nonetheless, if progress is to be made, this taxon must be fitted, however roughly, into the general system of theory about phylogeny in the American tropics. Evidence is derived from two sources: holomorphology and chorology.

Stated simply, the general pattern of evolution in the northern Neotropical Region involves differentiation, dispersals and redispersals between South and Middle America during favorable times, and survival in various refugia during less favorable times. Superimposed on this is development of montane-adapted stocks from lowland ancestors (Whitehead 1976; see his paper for additional references about this topic).

Structural features of *Anisocnemus* make it clear that adults are selenophorine burrowers in soil, and limited observations of living individuals tend to confirm their burrowing habits. Because burrowers are the exception rather than the rule among harpalines in general and selenophorines in particular, it seems likely that burrowing is an apotypic feature, and characters associated with it are apotypic, too. (Following the classification of phylogenetic methods by Eklis [1977:125], this is application of the criterion of frequency of occurrence and the criterion of adaptive significance). Thus, either *Anisocnemus* is descended from a non-burrowing ancestor, or shared a common ancestry with another group of burrowers.

Adults of *Discoderus* are also burrowers, but this genus and *Anisocnemus* are not strongly linked by synapotypic features that are independent of burrowing adaptations. The enlarged sternum 10 might be such a character state, but this could just as easily be the result of convergence. Furthermore, adults of *Discoderus* share some derived character states with some members of one species group of *Selenophorus*, and thus might share a common ancestry with those species. So, we are not prepared to suggest a close relationship between *Discoderus* and *Anisocnemus*. Rather, we believe that the two groups are derived independently from surface-inhabiting ancestors.

Features shared with adults of other groups, such as lack of setigerous punctures from stria 7, we believe to represent losses, and such could have taken place independently in each group thus characterized. Furthermore, such loss might also be related to the burrowing mode of existence, for selenophorines showing it (members of *Stenomorphus* and most species of *Trichopselaphus*) are also more or less modified as burrowers. But, at present, we lack the necessary evidence to identify the extant sister group of *Anisocnemus*.

In interpreting structural features of the species, we believe that the sinuate sides and rectangular hind angles of the pronotum of *A. validus* and the lack of adhesive vestiture from the middle tarsi of *A. amblygonus* are apotypic. Thus, each species has at least one autapotypic character state. Classification of both sets of characters is based on the criterion of frequency of occurrence. Additionally, evaluation of reduction of tarsal vestiture is based on the criterion of correlation with adaptive significance: this is a common feature of burrowing carabids.

We know nothing about the way of life of *A. validus*, so we cannot know if this species and *A. amblygonus* differentiated with respect to ecological characteristics. However, because the middle tarsi of males of *A. validus* have adhesive vestiture, we suspect that members of this species are less subterranean than are members of *A. amblygonus*.

Because the center of diversity and divergence of selenophorines in the New World is the tropics, and because the range of *Anisocnemus* is confined to the tropics, we postulate that the center of origin of this genus is the Neotropical Region. We also think it most likely that this group arose in South America, rather than in Middle America.

The two extant species seem to be allopatric and are sufficiently similar to one another that they probably are not very old. Because they seem to be geographically separated from one another on opposite sides of a mountain range (the northeast-southwest trending Cordillera de Merida of the Andes), and because *A. amblygonus* is wide ranging in Middle America, and *A. validus* is confined to South America, we postulate that the species differentiated from a common ancestor whose populations survived in isolated refugia sometime during the late Tertiary or early Quaternary. It seems likely to us that the ancestral stock of *A. amblygonus* was in a Central American refugium, and that in recent time, the range of this species extended into northern South America, and into Mexico. Dispersal might have coincided with establishment of the Central American land bridge, though it need not have, for adults of this species seem to be strong flyers, and presumably they could have crossed water barriers. Alternatively, *A. amblygonus* could have evolved in South America, to the north of the Cordillera de Merida, and could have dispersed into Middle America fairly recently.

An example of a very similar distribution pattern is provided by the ant eater genus *Tamandua* Gray. The range of *T. mexicana* Saussure parallels that of *Anisocnemus amblygonus*, and *T. mexicana* is replaced in the trans-Andean region by *T. tetradactyla* Linnaeus (Wetzel 1975). Kingsolver and Whitehead (1976:329-331) recognized seven distribution patterns based on northern and southern distribution limits of tropical American taxa of bruchid beetles. The pattern of *A. amblygonus* is in Category 6 in Kingsolver and Whitehead's system.

Thus, the distribution pattern of *Anisocnemus* species fits the pattern that seems general for taxa that inhabit lowlands of the northern portion of the New World Tropics, i.e., minor differentiation and allopatric ranges, with the Middle American vicar wideranging, and exhibiting only slight geographical differentiation. This correlation does not prove the validity of the explanatory hypothesis for evolution of the overall pattern, but it does lend support. Identification of such correlations is a major justification for studies of this kind, involving, as they do, taxa of doubtful significance to the economy of men.

In conclusion, we have presented a hypothesis to be tested. Of particular interest in this connection is the geographical distribution of the two species in northern South America. We need to know if they are, in fact, reproductively isolated. Of course, it would also be interesting to learn if there are other species of *Anisocnemus*, and if so, what bearing their character states and distribution patterns will have on our views about relationships and evolution of *Anisocnemus*.

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